Missouri
Botanical
Garden

## The Unseen Garden: Research at MBG

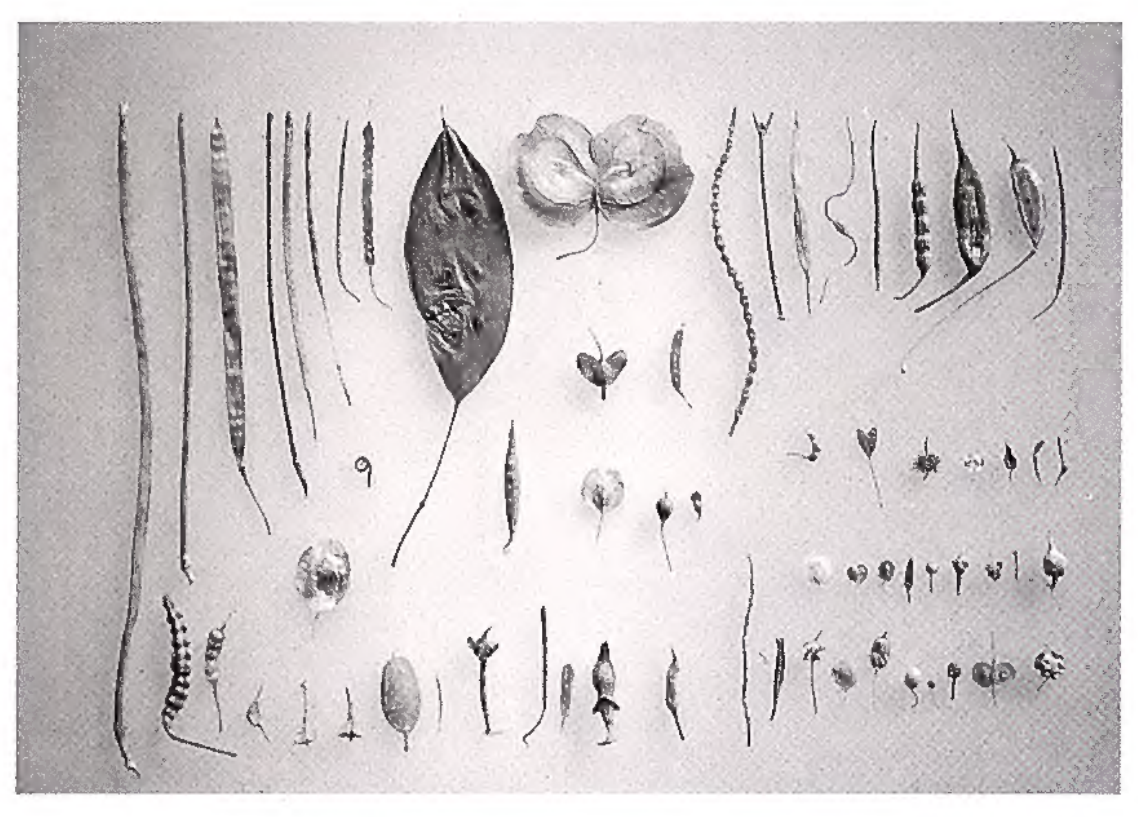
Plants are absolutely essential to sustaining the stability and quality of human life on this planet. Developing countries have 80% of the earth's biodiversity, but less than one in 10 of the world's scientists. With operations in over 30 countries around the globe, the Missouri Botanical Garden's Research Division is working to change that statistic. MBG botanists collaborate with local institutions in each country where they conduct research and field work, provide technical expertise, assist with fundraising, establish better communication with the worldwide scientific community, train botanists in the field and at MBG, and help to build infrastructure.

The MBG Research division consists of 45 Ph.D.-level botanists assisted by 100 technical and support staff and 34 graduate students. Their studies are concentrated on the plants of Mesoamerica, South America, Subsaharan Africa, Madagascar, China, Vietnam, and North America. Individual MBG scientists are specialists in the plants of particular regions, in the systematics and evaluation of major plant families, and in the interactions between plants and people.

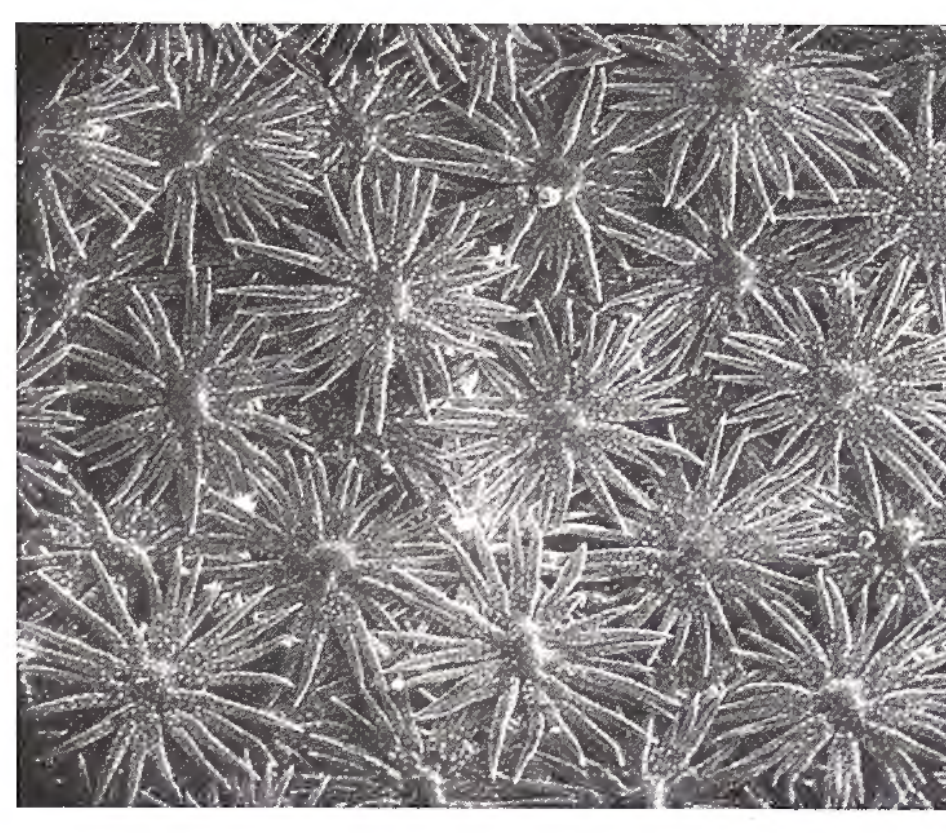
MBG serves as headquarters for the U.S. Center for Plant Conservation and for several major collaborative publications, such as the *Flora of China, Flora Mesoamerica, Flora of North America, Flora of Pakistan, Flora of the Venezuelan Guayana,* and others.

## The Brassicaceae Family: a Technical Overview

The Brassicaceae (Cruciferae), mustard family, *sensu stricto*, consists of about 340 genera and some 3,400 species distributed worldwide. Molecular and cladistic studies support the monophyly of the family and indicate that it is most closely related to other families that contain glucosinolates. These families collectively form the well-defined order Brassicales. Such studies also clearly demonstrate that the Brassicaceae is a sister group of the subfamily Cleomoideae of the Capparaceae, and that the two families should be united in one (Brassicaceae), a position well supported by most students of systematic and evolutionary botany. Therefore, the Brassicaceae *sensu lato* include three subfamilies: Brassicoideae (mustards), Cleomoideae (Cleome and relatives), and Capparoideae (cappers and relatives). This account will deal only with mustards.


Fruit diversity in the Brassicaceae

**Morphology.** The Brassicaceae are herbs almost two-thirds of which are perennials, and only about two percent of the species are shrubs that belong to 16 genera. Shrubby habit evolved independently several times in the family. Vines or climbers are known in three unrelated genera: the South American *Cremolobus*, the Australian *Lepidium*, and the South African *Heliophila*. All members of the family have a watery sap with glucosinolates that, upon crushing the fresh parts, are hydrolyzed by the enzyme myrosinase to yield the pungent, hot isothiocyantes. The leaves are simple (pinnately or palmately compound in some *Cardamine*), alternate (rarely opposite in *Lunaria* and some *Cardamine*, or whorled in some *Taphrospermum*), and estipulate. The trichomes are almost exclusively unicellular, and their types are extremely important in the separation of species and genera. The flowers are actinomorphic (zygomorphic in some *Iberis* and *Streptanthus*), bisexual, and mostly arranged in racemes (on solitary pedicels from rosettes in *Idahoa* and *Solms-laubachia*). The sepals are free (united in 12 genera, but these evolved independently), and the four petals form a **cruciform** corolla (hence the earlier family name Cruciferae), though the petals are absent in many species of *Lepidium*. The stamens are mostly **tetradynamous** (the two inner median pairs are longer than the outer lateral pair), but they are equal in length (*Warea, Stanleya*), in three pairs of unequal length (several *Streptanthus*), reduced to two (many *Lepidium*), or 16–24 (*Megacarpaea polyandra*). The pollen is tricolpate in 96% of the family, but in seven genera and about 135 species (*Physaria* and relatives) the pollen is 4–11-colpate. The **nectar glands**, which are always present on the receptacle at the bases of lateral stamens and sometimes also at those of median stamens, have been used frequently in generic delimitation. The fruits are 2-valved (3–6-valved in *Rorippa barareifolia* and *Tropidocarpum capparideum*), 2-loculed (with a septum separating the two parietal placentas; septum is lacking in several genera) capsule often dehiscing longitudinally (indehiscent in about 50 genera) and leaving behind the **replum** (placental frame) and **septum**. Their shape, compression, and modification are extremely useful in the separation of genera and species. The term silique is used when the fruit is greater than 3 times longer than wide and silicles when less than 3 times longer than wide), but such distinction is artificial and has no phylogenetic implications. Indehiscent, nutlike (*Zilla*), schizocarpic (*Cremolobus, Menonvillea*), samaroid (*Isatis, Thysanocarpus*), or lomentaceous (*Enarthrocarpus*) fruits are also found. The seeds contain no albumin and the embryo is oily, occupies the entire seed, and **strongly curved**. The type of curvature of the radicle in relation to the cotyledons is often useful taxonomically. Seed germination in the family is epigeal.


Leaf hairs of Physaria hichcockii

**Distribution.** The centers of greatest diversity of the family include the Irano-Turanian region (Turkey and Syria east into Tajikistan, Kyrgyzstan, and southern Kazakstan) has about 150 genera (60 endemic) and approximately 900 species (530 endemic), North America has 100 genera (40 endemic) and 800 species (nearly 690 endemic), and the Mediterranean region has about 110 genera (20 endemic) and 630 species (290 endemic). Other smaller centers include South America (42 genera, 30 endemic; some 390 species, 340 endemic), the Saharo-Sindian region (north Africa, Arabian Peninsula, into southern Iran, and Pakistan) (65 genera and 180 species) South Africa (15 genera and nearly 110 species), and Australia and New Zealand (19 genera and 120 species). All taxa of the southern hemisphere have evolved from ancestors in the northern hemisphere. There is a disagreement about the home origin of the family, though it is likely that it was in the Old World.

*Zilla spinosa*

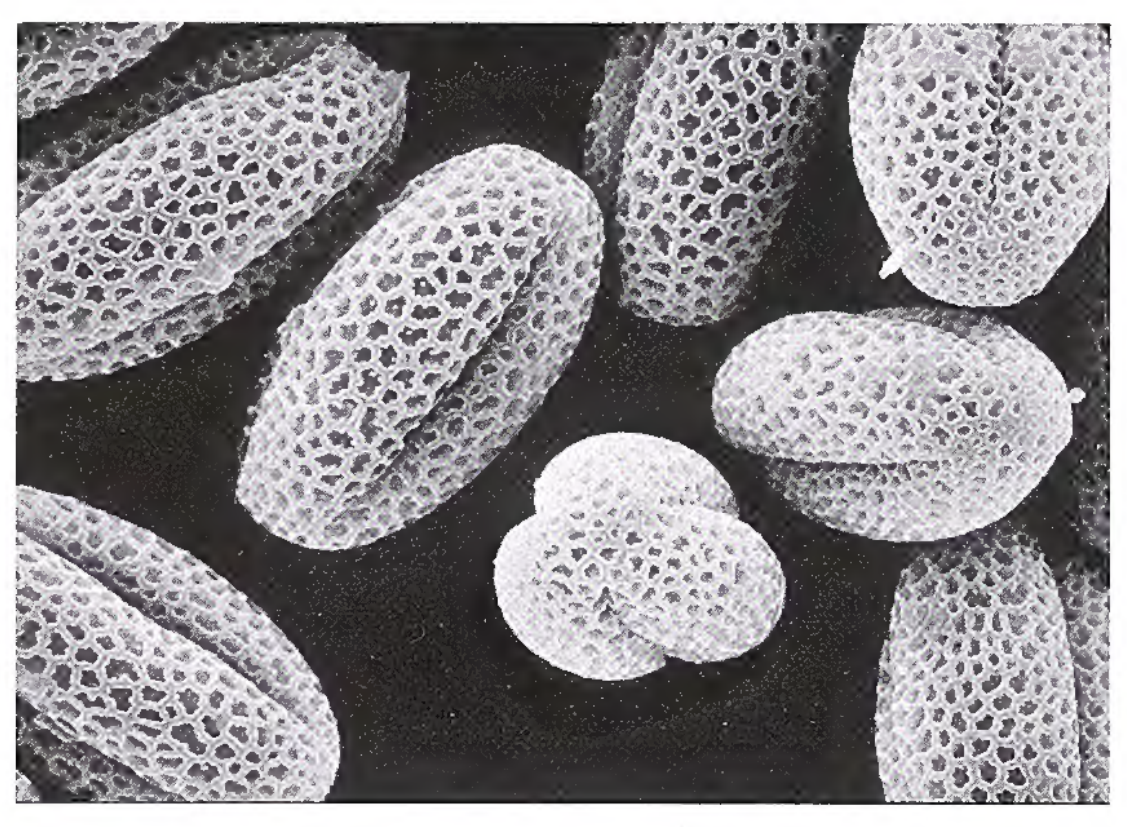
**Habitats.** Species of the Brassicaceae grow primarily in the arid and semi-arid temperate areas of all continents, though numerous *Draba* are well established in the alpine and subalpine areas and at northern latitudes (70–80°N) well into the Arctic Circle. Many species of *Draba* and other genera flower while parts or most of the plant is still covered with snow. In fact, the Himalayan *Lepidostemon everstianus* grows at elevations of about 6,400 meters (21,000 feet) along the northern slopes of Mount Everest, and very few vascular plants can survive at such high altitudes. Species of many genera grow in mesic habitats, but deserts are the homelands of a vast majority of Brassicaceae. The thorny desert shrub *Zilla spinosa* (Middle East and northern Africa) sheds its leaves at the onset of the dry season, and the green thorns and stems become the photosynthetic organs. Species of a few genera (e.g., *Cardamine, Nasturtium, Rorippa, Subularia*) are successful submerged aquatics, and those of the sea rocket (*Cakile*) are strand plants that grow almost exclusively along sandy beaches beyond the reach of high tides.

**Dispersal.** Seeds and indehiscent fruits are dispersed by wind, water, or animals, and each type of dispersal evolved independently several times within the family. In most species dispersal is limited to short distances, but small seeds are easily washed by rain or dispersed by wind. Wind dispersal is most common in species with winged seeds (*Arabis*), samaroid fruits (*Isatis*), inflated bladder-like fruits (*Physaria*), and dust-like seeds of some desert species (e.g., *Diplotaxis*, which are less than 0.5 mm long and weigh as little as 0.05 mg). The Central Asian *Megacarpaea gigantea* has the largest seeds in the family (up to 1.5–1.8 cm), but these are enclosed individually in broadly winged fruit halves that are dispersed by wind. In the majority of the family, however, the seeds are generally small and rarely do they reach 4 mm in length. The Rose of Jericho or resurrection mustard (*Anastatica hierochuntica*), which is distributed along a stretch of 8,000 km from the hot deserts of Mauritania in northwestern Africa through the Middle East into Pakistan, loses its leaves in the dry season, curls up, breaks off the ground, tumbles for long distances, and readily expands and sheds its seeds when exposed to rain.

Dispersal by rain wash is quite common among species with small seeds, but typical dispersal by water currents is found in about a dozen species of aquatic plants (e.g., *Subularia aquatica, Rorippa aquatica, Nasturtium officinale*). Corky fruits of the six maritime species of *Cakile* and *Crambe maritima* are dispersed by floating on seawater.

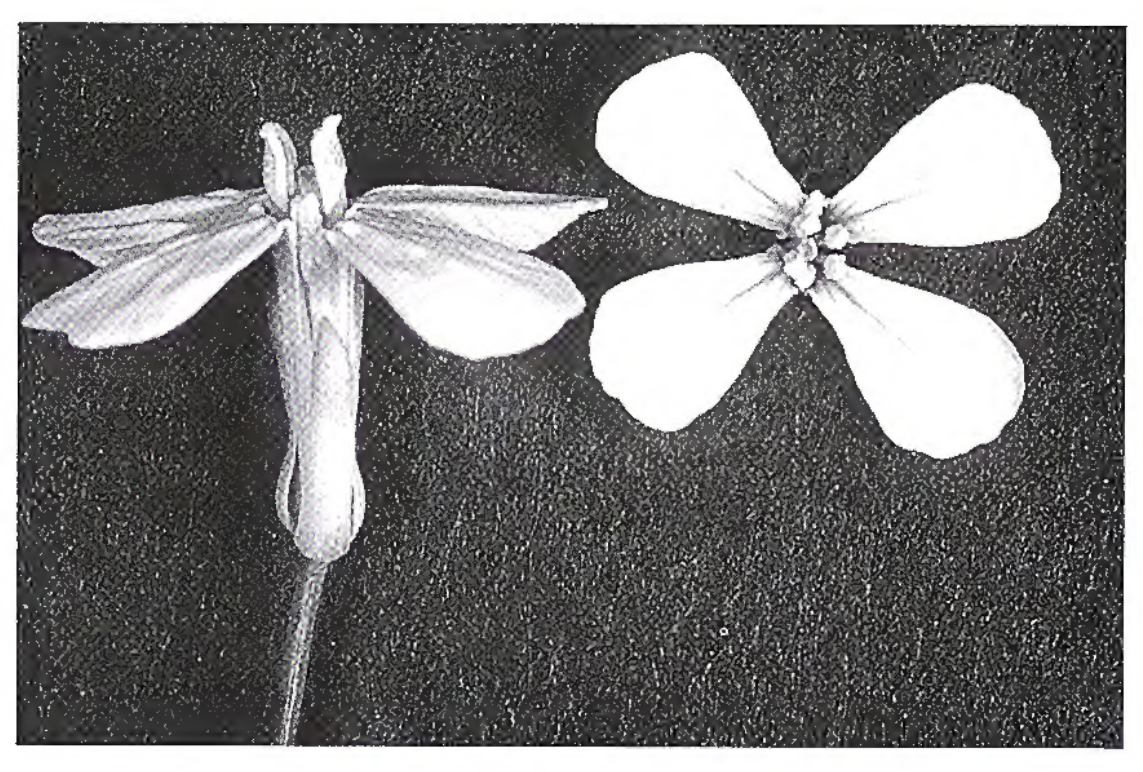
In numerous species the seeds readily release mucilage when wetted, and this helps them adhere to the soil or stick them to the feathers of birds or fur of mammals. Long-distance dispersal of *Lepidium* seeds by birds is attributed to the presence of abundant mucilage in the epidermal layer of seeds coat. Species that produce fruits with hooks (*Tauscheria*), spines (*Pugionium*), glochidiate trichomes (*Clypeola*), or sticky glands (*Parrya*) are dispersed by animals, but this type of dispersal is rather uncommon in the family.

A rare type of dispersal in the Brassicaceae is geocarpy, which evolved independently in the South American *Cardamine chenopodiifolia*, Australian *Geococcus pusillus*, South European (Corsica, Sardinia) *Morisia monanthos*, and a few species of the Himalayan *Lignariella* and *Pegaeophyton*. In these species, the fruiting pedicel bends downward and buries the fruit next to the parental plant.

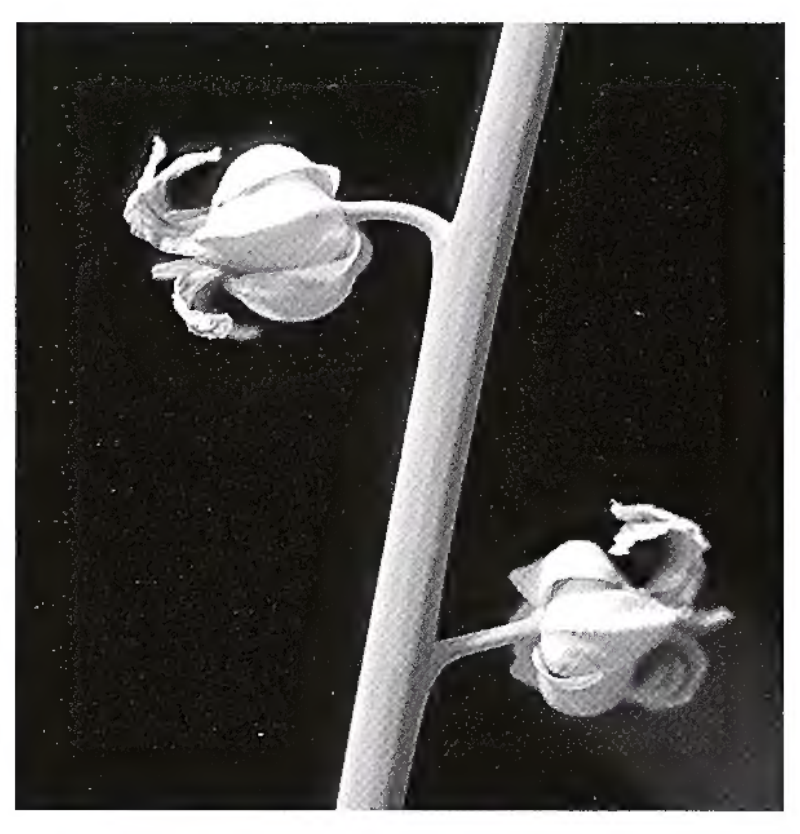

Pollen of Streptanthus carinatus

**Pollination.** The Brassicaceae are generally pollinated by Hymenoptera (bees), Diptera (flies), Lepidoptera (moths and butterflies), and rarely by Coleoptera (beetles). Species pollinated by moths and butterflies often have pollen with a rather coarsely reticulate surface. Wind pollination is known only in *Pringlea antiscorbutica*, a species restricted to a few islands in the south Indian Ocean at latitudes 45–55°S. Self-pollination is quite common in the family, especially in weedy taxa and in species with cleistogamous flowers (*Subularia aquatica, Draba* spp.). Protogyny is widespread in the family, while protandry is extremely rare (*Streptanthus*), and dioecism is known only in *Lepidium sisymbrioides* of New Zealand.

**Generic limits.** The Brassicaceae are taxonomically difficult at the generic rank because many genera are delimited primarily on the basis of a few characters. Unique characters (e.g., fimbriate petals in *Ornithocarpa*) are quite rare, and convergence is known in almost every conceivable character. Generic lines often follow tradition rather than being based on sound phylogenetic studies. Recent molecular data support the merging of what appears to be superficially distinct genera (e.g., *Lepidium* includes *Cardaria, Coronopus, Hymenophysa,* and *Stroganowia*; *Vella* includes *Boleum* and *Euzomodendron*) or the splitting of genera that appear to be uniform morphologically (e.g., *Arabis*). Well-established genera, such as *Brassica, Erucastrum,* and *Diplotaxis*, are artificially delimited, and perhaps they should be united.


*Brassica napus*

The eight largest genera in the Brassicaceae (about 40% of the total) all appear to be monophyletic. These include *Draba* (about 350 species: north temperate and the Andes of South America), *Lepidium* (about 220: worldwide), *Cardamine* (about 200: worldwide), *Alyssum* (170–190 species: Eurasia), *Erysimum* (about 180: primarily Eurasia, 16 species in North America), *Physaria* including *Lesquerella* (110: North America, a few disjunct in South America), *Heliophila* (80: South Africa), and *Rorippa* (75: worldwide). The majority of genera (250) include one to five species, and nearly half of these (130 genera) are monotypic (with one species). It is highly possible that the number of monotypic genera will be drastically reduced, especially after their phylogenetic relationships are fully resolved. Only the genera *Cardamine, Lepidium,* and *Rorippa* are represented by indigenous species on all continents except Antarctica.


*Streptanthus albidus*

**Classification and phylogeny.** All of the tribal classifications proposed during the past 170 years are artificial. Between two and 19 tribes and 30 additional subtribes have been recognized. These classifications are based primarily on a few characters (e.g., types of nectar glands, fruit compression, trichomes, cotyledonary position, and fruit length in relation to width) and on the assumption that most, if not all, characters have evolved only once. Homoplasy occurs in almost every conceivable character in the family, and it is almost impossible to construct phylogenies based entirely on morphology. Molecular data reveals that perhaps the tribe Brassiceae (ca. 50 genera and 230 spp., primarily Mediterranean) and Heliophileae (1–6 genera and ca. 80 spp., exclusively south African) are monophyletic. Synapomorphies that define the Brassiceae are conduplicate cotyledons and/or segmented (heteroarthrocarpous) fruits, whereas the Heliophileae share diplecolobal cotyledons. The rest of the family cannot be meaningfully divided into large monophyletic groups. Perhaps a better approach would be to divide the family into smaller clades based on synapomorphies and comprehensive, family-wide molecular data combined with critical analysis of morphology. Extensive phylogenetic studies using various nuclear and chloroplast markers are being conducted in laboratories in the United States, Canada, Germany, Austria, and elsewhere. We now have a much better understanding of phylogeny and delimitation of genera such as *Arabidopsis, Arabis, Boechera, Brassica* and all its allies, *Cardamine, Capsella, Cochlearia, Draba, Heliophila, Lepidium, Nasturtium, Noccaea, Physaria, Rorippa, Sisymbrium, Thlaspi,* and *Yinshania*, as well as many others in progress.

*Brassica oleracea var. acephala*

### Photo Credits:

Front from top: *Stanleya pinnata* by Mark Olson. *Heliophila* sp. by Klaus Mummenhoff. *Thysanocarpus curvipes* by Robert A. Price. *Heliophila arenaria* by Kalus Mummenhoff. *Erysimum capitatum* by Dean W. Taylor. *Christolea crassifolia* by Ihsan A. Al-Shehbaz. Landscape with *Lepidium jaredii* by Dean W. Taylor.

Back: Fruit diversity in the Brassicaceae by Ihsan A. Al-Shehbaz. Pollen of *Streptanthus carinatus* by Ihsan A. Al-Shehbaz. Leaf hairs of *Physaria hitchcockii* by Umesh Banerjee. *Streptanthus albidus* by Dean W. Taylor. *Brassica napus* by the Chicago Biological Supply House. *Zilla spinosa* by Fernand Jacquemoud. *Brassica oleracea var. acephala* by Ihsan A. Al-Shehbaz. Photo of Dr. Ihsan A. Al-Shehbaz by Trent Foltz.

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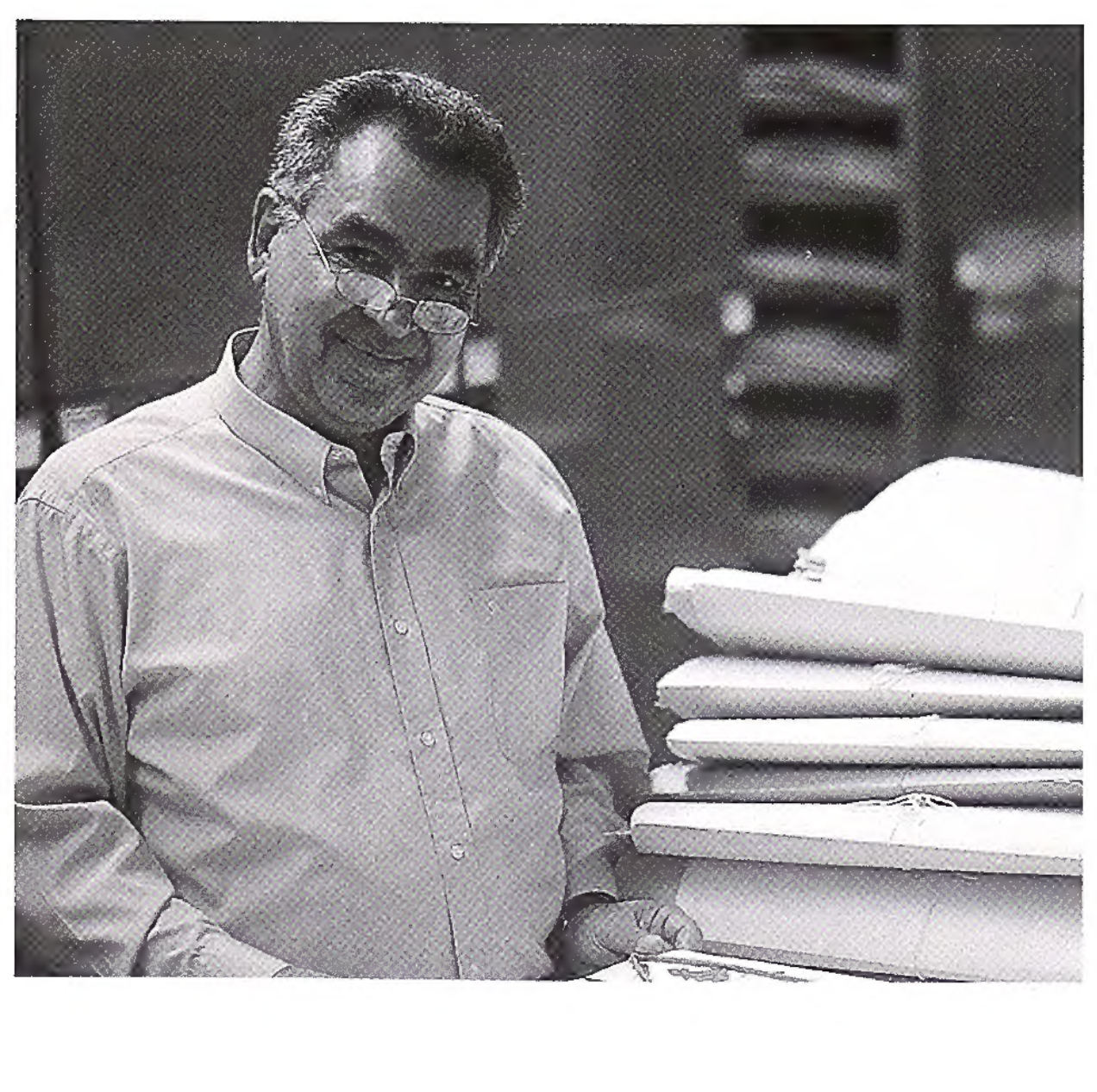


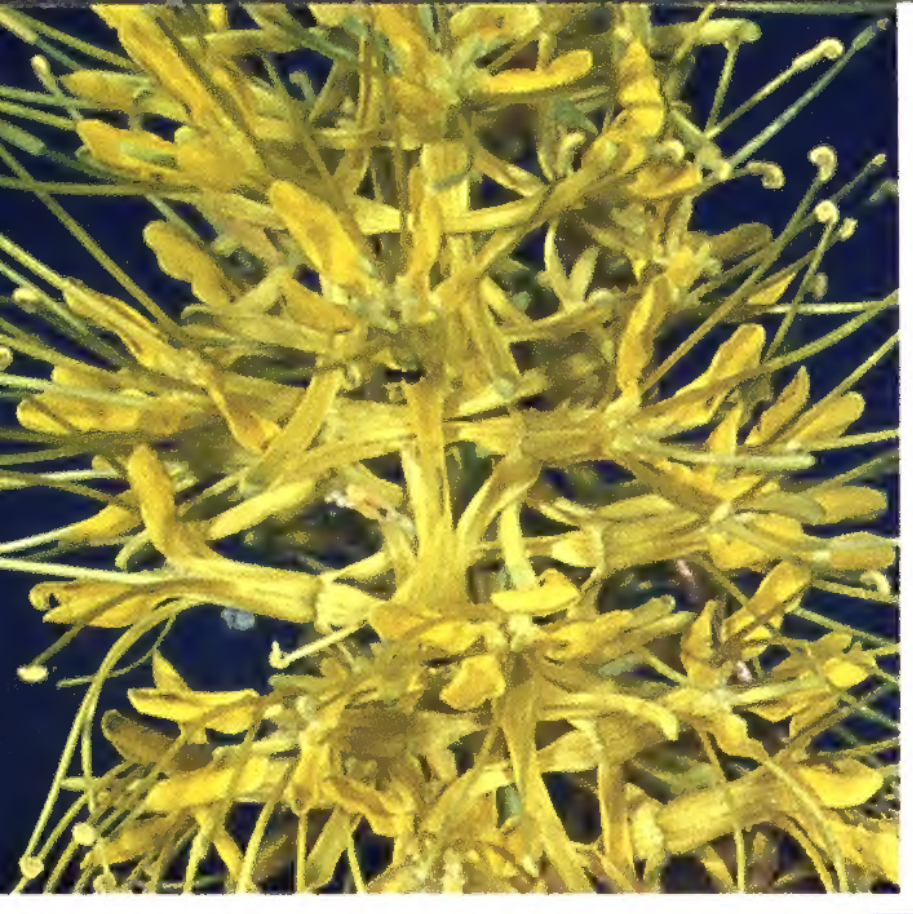
### About the Author:

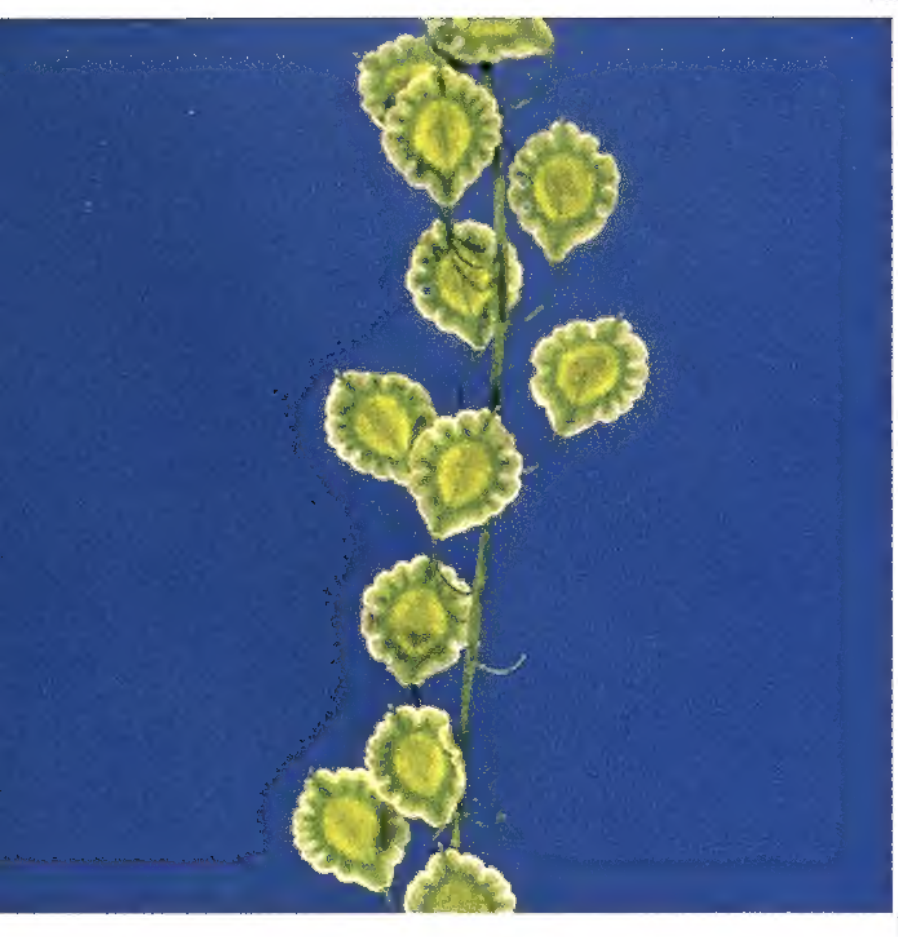
MBG Senior Curator Ihsan A. Al-Shehbaz is an internationally renowned expert on the systematics and evolution of Brassicaceae, the mustard family. He has described more than 110 species and 12 genera new to science. In addition to his work on the mustard family, he also heads the Department of Asian Botany, including supervision of the *Flora of China* project and the Garden's activities in Vietnam and elsewhere in Asia. He conducts field work in China and Central Asia and supervises graduate students working on the mustard family.

Research at the Missouri Botanical Garden

# Mustards

## (Brassicaceae)





Members of the mustard family, Brassicaceae, are distributed on all continents except Antarctica, but the greatest number of species grow in three major regions: southwestern and central Asia, western United States and northern Mexico, and the Mediterranean region. Mustards are easy to distinguish by their flowers, which feature four separate petals arranged in the form of a cross, thus the other name for the family Cruciferae from the Latin for cross.

Many kinds of mustards have considerable economic importance, including vegetable crops, ornamentals, sources of edible and industrial oils, and spices. It is believed that the ancestors of cabbage were grown in coastal Europe some 8000 years ago, and some crops of the genus Brassica were domesticated as far back as 3000 B.C., as evidenced by Sanskrit records in India. Roots, stems, leaves, and flowers of crop mustards are eaten raw, stewed, cooked, pickled in vinegar, or fermented in brine. The vegetables include everything from broccoli and cauliflower to radishes and turnips to a variety of salad greens (see table below). All of these vegetables are high in vitamin C and are excellent antioxidants. Table mustard is manufactured primarily from a mixture of the seeds of *Sinapis alba* (white mustard) and *Brassica juncea* or *B. nigra* (Indian and black mustard, respectively). These seeds are also used as a spice in the seasoning of foods and in pickling. The grated fleshy roots of the European horseradish and Japanese wasabi yield the hot condiments that are popular primarily in the West and eastern Asia, respectively.

Seeds of several crop mustards are rich in oils—some with an oil content as high as 40%. Canola oil is extracted from rapeseed, and other vegetable oils more popular in Asia are obtained from other species of mustards. Besides cooking, mustard oils are used in the manufacture of all-purpose grease and lubricants, margarine, varnishes, lacquers, soft soap, resins, plastics, nylons, pharmaceuticals, vinyl stabilizers, synthetic odors and flavors, floatation agents, and insect repellents. Even the waste is useful: the seedcake left after oil extraction has a protein content of 20–35% and is frequently used as fertilizer or animal feed. Mustard oils rank among the top two or three crops in the world's overall tonnage production.

In addition to food and oil production, the mustard family is also a star player in botanical research. Perhaps the best-known experimental organism in botanical science is the little Eurasian weed *Arabidopsis thaliana* (thale cress or mouse-ear cress). This species, which is sometimes called the drosophila of the plant kingdom after the famous fruit fly species used in genetic research, has become the model plant in experimental biology for its many superior qualities. Thale cress is used in numerous research areas, including disease resistance, crop improvement, plant genetics, physiology, development, evolution, ecology, and population biology, to name a few. Almost every major university has one or more scientist working on this plant. It is one of only a few organisms on Earth to have its entire genome sequenced. Extensive efforts are being made to identify its various genes and the processes they control.

In the home garden, several mustards are grown primarily for their attractive characteristics. Such ornamentals include the honesty or money plant, stock, and wallflower, and of course, ornamental cabbage—a compact colorful form of kale. There are some noxious members of the family, however. Brassicaceae includes about 50 genera with over 120 species of weeds. In fact, the second most common weed on Earth is a mustard—Shepherd's purse, *Capsella bursa-pastoris.*

From research to horticultural display to industrial use, the mustard family is far more diverse and valuable than its well-known role as condiment might suggest.

### MUSTARD TRIVIA

- Mustard produces about 1,000 pounds of seeds per acre.
- Most of the mustard seeds used in Dijon, France are grown in United States and Canada. Canada produces about 90 percent of the world's supply of mustard seeds.
- Over 700 million pounds of mustard are consumed worldwide each year.
- More than 1,600 gallons plus 2,000,000 individual packets of mustard are consumed annually at Yankee Stadium.
- George J. French introduced his French's mustard in 1904, the same year the hot dog was introduced to America at the St. Louis World's Fair.

Members of the mustard family are among the most common vegetables on the dinner table. Included in *Brassica oleracea* are cabbage (var. *capitata*), cauliflower (var. *botrytis*), broccoli (var. *italica*), Brussels sprouts (var. *gemmifera*), kohlrabi (var. *gongylodes*), and kales and collards (var. *acephala*). Other significant crops include rutabaga (*B. napus* var. *napobrassica)* and turnip (*B. rapa* var. *rapa*), as well as numerous leafy vegetables such as Chinese cabbage (*B. rapa* var. *glabra* and var. *chinensis*) and Indian mustard (*B. juncea*). The humble radish (*Raphanus sativus*) is also a member. In addition, several salad greens are members of the mustard family, including watercress (*Nasturtium officinale*), cress (*Lepidium sativum*), and arugula (*Eruca vesicaria* subsp. *sativa*).